

## CONSEQUENCES OF MATE SHARING FOR FIRST-MATED FEMALES IN A POLYGYNOUS SONGBIRD, THE HOUSE WREN

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**ABSTRACT.**—We investigated whether male parental assistance, reproductive output, and overwinter survival differed for female House Wrens (*Troglodytes aedon*) that did and did not have to share their mate's territories with a later-settling female during the nestling stage of breeding. During first breeding attempts of the season, when mate sharing occurred, primary females in polygynous trios and females from monogamous pairs fledged equal numbers of offspring and fledged offspring of similar mass. Rates at which males fed broods of primary females were not significantly different than rates at which males fed broods of monogamous females. Primary females did not make significantly more trips to nests to feed offspring than did monogamous females. In the first year of study, primary females were more likely than monogamous females to attempt a second brood. In the second year of the study, however, primary females tended to be less likely to attempt a second brood, took longer to start such broods, and tended to be less successful in fledging offspring from second broods. This suggests that in some years there may be a delayed cost of mate sharing. Females with primary and monogamous status for first breeding attempts in a particular year were equally likely to return to the study area the next year. Overall, our results indicate that mate sharing does not appear to affect the reproductive output of first mated females in our House Wren population in the first breeding attempts of the season, but may affect output in second attempts (and hence possibly annual and lifetime success), at least in some years. *Received 15 March 1999, accepted 20 Oct. 1999.*

Avian polygyny has been intensely studied for nearly four decades. The vast majority of studies have focused on determining why females sometimes settle with mated males, given the potential costs of mate sharing for a secondary mate (Searcy and Yasukawa 1989, Johnson et al. 1993, Slagsvold and Lifjeld 1994). Far less attention has been given to how mate sharing affects first mated or "primary" females, yet such information should be of value in understanding the evolution of avian mating systems in general (Davies 1989). For example, the widespread occurrence of monogamy in birds may result from first mated females routinely discouraging other females from settling on their mate's territory (Wittenberger and Tilson 1980, Gowaty 1995, Sandell 1998). This female-female aggression hypothesis for monogamy assumes that the presence of a secondary female on a territory is in some way costly to the primary female. Few studies have documented the nature and extent of these costs.

Potential costs of mate sharing (Bensch 1997) for primary females include: (1) competition for food, nest sites, and other resources

on the male's territory; (2) reduced male assistance incubating eggs and feeding offspring because males spend time tending to the secondary female and her brood (Lifjeld and Slagsvold 1989, Pinxten et al. 1993, Sandell et al. 1996); (3) less male help watching for predators and defending nests (Hannon 1984); (4) increased exertion resulting from attempts to compensate for loss of male assistance in incubating eggs or brooding or feeding offspring (Johnson and Kermott 1993, Pinxten et al. 1993, Pinxten and Eens 1994); (5) destruction of eggs or offspring by secondary females (Veiga 1990, Bensch and Hasselquist 1994, Hasson et al. 1997), which selection should encourage because males usually shift parental attention fully to the secondary nest if the primary nest fails (Lifjeld and Slagsvold 1989, Johnson et al. 1993, Smith et al. 1994); and (6) relegation to secondary status if the primary female attempts to renege with her polygynous mate either after nest failure or for a second brood (Bensch 1996). These costs may ultimately reduce fitness of the primary female by reducing reproductive success in the current breeding attempt, future breeding attempts, or both, and by reducing the reproductive lifespan of the female.

Our objective was to assess the consequences of mate sharing for primary females

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in a polygynous population of House Wrens (*Troglodytes aedon*).

## METHODS

*Study species.*—House Wrens are small (10–12 g), sexually monomorphic, insectivorous, cavity-nesting songbirds (Johnson 1998). Wrens return to our Wyoming study site in early May. Males sing to attract mates, and females visit territories of different males and discriminate among potential mates at least partly on characteristics of nest sites that males control (Johnson and Searcy 1993, 1996). Females usually lay clutches of 4–8 eggs with clutch size declining seasonally. Only females incubate. Males usually begin advertising for secondary mates at unoccupied nest sites on their territories when their first mates begin regular incubation (with the laying of the penultimate egg; Johnson and Kermott 1991). About 15–35% of males mate polygynously each year when most males are provided with more than 1 nest box on their territories. Clutches begin hatching 11–13 days after the last egg is laid. Both parents feed nestlings. Offspring fledge 16–18 days after hatching and are fed by one or both parents for 2 weeks thereafter.

*Study site and general methods.*—We conducted this study in 1996–1997 on a population of House Wrens nesting in riparian woodlands near Big Horn, Wyoming (44° 40' N, 106° 56' W, 1310 m). All wrens in this study were individually marked with unique combinations of colored leg-bands. We provided wrens with nest boxes mounted 1.25–1.75 m above ground on greased metal poles. Prior to wren arrival each spring, we erected two nest boxes, 25–45 m apart, on each of approximately 80 territories that had been occupied by males in previous years. Initially only one box was opened; the other was covered with a black plastic bag. We opened second boxes on the day that a male's mate laid egg 3, 4 or 5, i.e., a day or two before males normally begin advertising for secondary mates.

On many territories, the male did not attract a secondary mate by the time his first mate's eggs hatched. We were reluctant to leave extra nest sites open during first mates' nestling stages on all territories because, under natural conditions, not all males have access to a surplus nest site. A male with access to a surplus nest site during the nestling stage may modify his parental effort, putting less time into feeding offspring and more time into trying to attract an additional mate (Pinxten and Eens 1994, Smith 1995). In an earlier year when no boxes were on our site and all birds used natural cavities, about 60% of monogamous males had access to a second, natural nest cavity on their territories during their first mate's nestling stage (Johnson and Kermott 1991). We mimicked this situation by closing extra nest sites on about 40% of territories, chosen at random, starting 1–3 days before eggs began hatching on those territories.

On some territories, second boxes that we erected were claimed by "surplus" males. Such males were

trapped and removed before they paired as time permitted. In a few instances, however, a surplus male had a female building a nest in his box on the day that he was removed. Subsequently, the paired male nearby quickly claimed both the box and the female, thereby obtaining a secondary mate. Such usurpatory polygyny occurs naturally in House Wrens (Freed 1986) so we included first mates of males participating in usurpatory polygyny in our sample of primary females ( $n = 6$  of 38, 16% of primary females).

We counted numbers of offspring in nests on Nestling Days (NDs) 4, 8, 12, and 15 or 16 (where ND 1 = day on which eggs began hatching). We weighed nestlings on ND 12, the day that first-hatched offspring are at or near their maximum weight. In Illinois, nestling House Wrens that are relatively heavy on or near this day are more likely to survive to breed (C. F. Thompson, pers. comm.). In 1996, nestlings in each brood were weighed collectively to the nearest 0.1 g using a spring balance. In 1997, we switched to weighing nestlings individually to the nearest 0.01 g using an electronic balance. This allowed us to compare primary and monogamous females from 1997 not only in mean mass of nestlings produced, but also in the number of nestlings produced whose ND 12 mass was at or above the mean ND 12 mass of all nestlings fledged that year. The latter measure may provide a better indicator of how many surviving offspring a female produces in a given year, given that broods often contain nestlings that vary substantially in mass.

*Parental effort.*—To obtain an index of feeding effort, we documented number of feeding trips to nests by each sex during 1 h observation sessions on NDs 2, 4, 9, and 15. Number of feeding trips is equivalent to number of prey delivered because parents deliver one prey per trip (Johnson 1998). We concentrated our efforts on the early nestling stage because females brood offspring extensively at this time leaving males to provide offspring with much of their food. We observed parental feeding rates throughout the nestling stage at all primary nests each year and at as many simultaneously active monogamous nests as possible. We chose monogamous nests for observation opportunistically (e.g., many were near primary nests, minimizing our travel time). Most monogamous nests that were not observed in the early nestling stage were observed once on ND 15 or 16 to allow us to compare rates at which males deserted monogamous and primary broods before offspring fledged. Mate desertion is common in this species and is described elsewhere (Johnson 1998 and references therein). To control for diurnal variation in parental behavior, we observed nests only in the early and mid-morning hours and timed watches so that the mean start time of watches at monogamous and primary nests were similar for any given ND.

*Reproductive output.*—We excluded from analyses females whose nesting attempts failed during the laying or incubation stages. Almost all of these females still had monogamous status at the time of failure. To include these females in our pool of monogamous fe-

males when comparing reproductive success of primary and monogamous females would be misleading. More specifically, it allows for a greater rate of failure for monogamous females than for primary females. This is because males who acquire second mates normally do so during the late laying or incubation stage of breeding (32 of 36 cases in this study). Thus many primary females in our study became primary females only because their nests remained intact through much or all of the incubation stage. To make an accurate comparison of the consequences of mate sharing, we included in analyses only females who: (1) completed incubation and (2) began the nestling stage either with monogamous or primary status. This meant that we also excluded from analyses the four primary females who became primary females unusually late; i.e., well into their nestling stage.

In our population, only females who began their first breeding attempts relatively early in the season attempted a second brood. In comparing the frequency with which monogamous and primary females attempted second broods, we included in our analyses all monogamous and primary females who fledged at least 1 nestling from first broods and who presumably began first broods early enough in the season to attempt a second brood. This included all females who began their first breeding attempt on or before the day the last female to attempt two broods that year began her first breeding attempt (all females who laid their first egg for first broods on or before 3 June in 1996 and 2 June in 1997). Masses of nestlings produced in second attempts were not compared because we were unable to obtain nestling masses for many second nesting attempts.

*Statistical analyses.*—We compared frequencies using log-linear  $G$  tests with Williams' correction. We compared measures of parental effort using two-way ANOVA which included pairing status and year as main effects. Clutch size and other measures of reproductive output declined as the breeding season progressed. When necessary, we controlled for seasonal effects on reproductive output in two ways. First, we included in analyses only monogamous females who began laying on or before the day the last primary female of the season began laying (8 July in 1996, 5 July in 1997). Second, we compared reproductive output using analysis of covariance (ANCOVA) with date of first egg as a covariate. When ANCOVA was used, we present least-squares means; i.e., means that are directly comparable because they have been adjusted to account for differences between monogamous and primary females in time of breeding. Where possible, data for our two years were combined in a single analysis that controlled for effects of year on reproduction. In most situations, however, we encountered a significant interaction between year and pairing status (monogamous females bred more successfully in one year and primary females in the other year). This forced us to examine the effect of pairing status on reproductive output in the two years separately. We used the Statis-

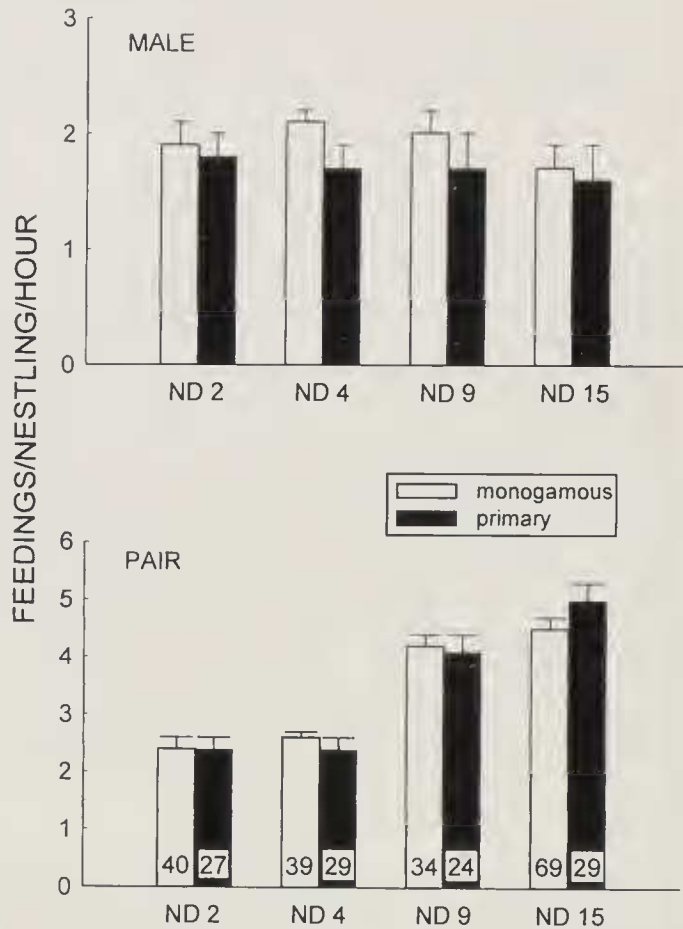


FIG. 1. Number of feedings per nestling per h at nests of monogamous and primary female House Wrens on different days of the nestling stage. Shown are means  $\pm$  1 SE with number of nests observed inside the lower bars. On Nestling Days 2, 4, and 9, none of the differences in means was significant when compared with a two-way ANOVA including year and female pairing status as main effects (all  $P > 0.05$ ). On Nestling Day 15, non-normal distributions precluded use of ANOVA. Because feeding rates at nests of each pairing status differed very little between years, data for both years were combined and compared using a Wilcoxon rank sum test (male rates) or  $t$ -test (pair rates). Differences were not significant (all  $P > 0.05$ ).

tical Analysis System (release 6.09; GLM procedure) on a VAX 6000 for analyses (SAS Institute 1985).

## RESULTS

*Parental care.*—Males fed offspring in monogamous and primary nests at similar rates throughout the nestling stage (comparisons on NDs 2, 4, 9 and 15: all  $P > 0.05$ ; Fig. 1). Polygynous males whose secondary mates were presumably fertile did not feed primary nestlings at a significantly lower rate than did males whose secondary mates were presumably infertile (comparisons on NDs 2, 4 and 9, all  $P > 0.05$ ; Fig. 2).

The rate at which both parents combined

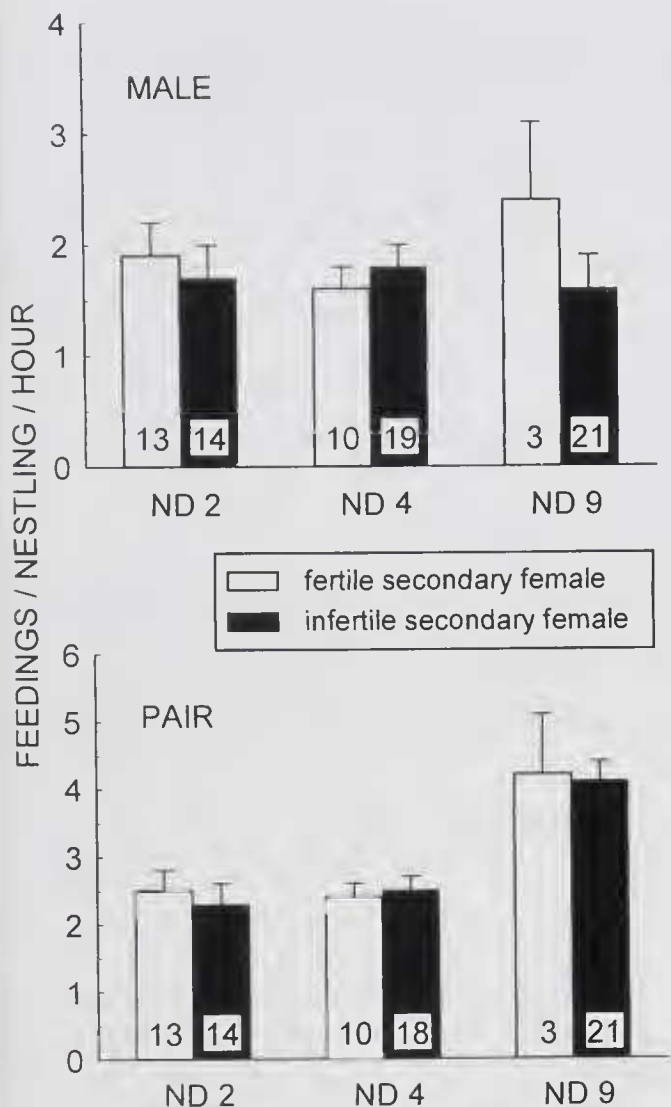


FIG. 2. Number of feedings per nestling per h at nests of primary female House Wrens when secondary females on the same territory were presumably fertile versus infertile. It was assumed that secondary females were fertile from the day that they paired through to the day that they laid their penultimate egg and began incubating. Shown are means  $\pm$  1 SE with number of nests observed inside the bars. None of the differences in means was significant when compared with a two-way ANOVA including year and secondary fertility status as main effects (all  $P > 0.05$ ). ND = Nestling Stage Day (ND 1 = day clutch begins hatching).

fed nestlings did not differ significantly at primary and monogamous nests (comparisons on NDs 2, 4, 9 and 15: all  $P > 0.05$ ; Fig. 1). We also found no significant difference in the effort that primary and monogamous females made to feed offspring as measured by total trips to nests with food, regardless of brood size (comparisons on NDs 2, 4, 9 and 15; all  $P > 0.05$ ; Fig. 3).

**Mate desertion.**—Males were equally likely to desert primary and monogamous females

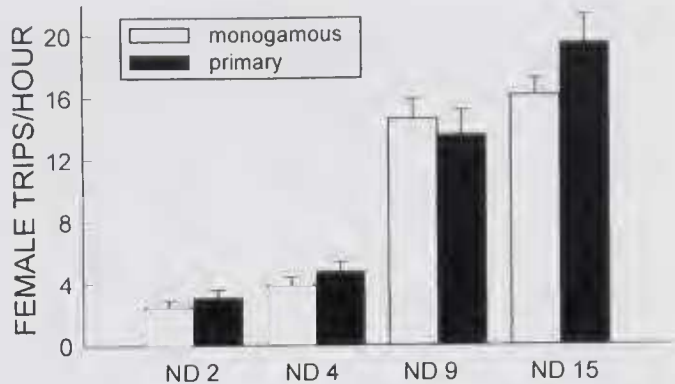


FIG. 3. Comparison of feeding effort (total trips to nest per h) by monogamous and primary female House Wrens on different days of the nestling stage. Shown are least-squares means  $\pm$  1 SE adjusted for effect of year. None of the differences in means was significant when compared with a two-way ANOVA including year and female pairing status as main effects (all  $P > 0.05$ ). Sample sizes match those in Fig. 1.

late in the nestling stage, being absent from 11 of 29 (38%) primary nests and 28 of 70 (40%) monogamous nests on ND 15 or 16 ( $G_1 = 0.04$ ,  $P > 0.05$ ). Desertion seemed unrelated to the degree of synchrony in reproductive cycles of primary and secondary females: the mean interval between hatching of primary and secondary clutches was 14.1 days on territories where males deserted primary broods and 15.3 days on territories where males did not desert ( $t_{27} = -0.72$ ,  $P > 0.05$ ).

Polygynous males were not more likely to have deserted the primary female by ND 15 or 16 if the secondary female had hatchlings by these days as opposed to unhatched eggs. Males deserted primary broods in 5 of 14 (36%) instances where the secondary female had eggs on ND 15 or 16 of the primary brood and 6 of 15 (40%) instances where the secondary female had hatchlings at this time ( $G_1 = 0.05$ ,  $P > 0.05$ ).

**Reproductive output in first breeding attempts.**—Clutches of primary females were significantly smaller than those of monogamous females in 1996 ( $F_{1,77} = 4.10$ ,  $P < 0.05$ ) and larger, although not significantly so, in 1997 ( $F_{1,88} = 2.42$ ,  $P > 0.05$ ; Table 1). Because clutch size would not have been related to mating status (males acquire secondary mates after first mates complete clutches), we included clutch size as a covariate in comparisons of number of offspring fledged by monogamous and primary females.

Primary females tended to be more likely

TABLE 1. Reproductive output of monogamous and primary female House Wrens during first breeding attempts of the season. Shown are the means  $\pm$  1 SE with number of nests observed in parentheses.

Measure	Year	Monogamous females	Primary females	Test statistic <sup>a</sup>	P
Date of first egg	1996	10 Jun $\pm$ 2 d (62)	31 May $\pm$ 3 d (18)	—	—
	1997	5 Jun $\pm$ 2 d (71)	6 Jun $\pm$ 4 d (20)	—	—
Clutch size <sup>b</sup>	1996	6.9 $\pm$ 0.1 (62)	6.4 $\pm$ 0.2 (18)	$F_{1,77} = 4.10$	<0.05
	1997	6.8 $\pm$ 0.1 (70)	7.0 $\pm$ 0.1 (20)	$F_{1,88} = 2.42$	>0.05
Percent nests successful <sup>c</sup>	1996	79.4 (68)	94.4 (18)	$G_1 = 3.57$	<0.06
	1997	80.0 (75)	90.0 (20)		
No. fledglings, all nests <sup>d</sup>	1996	4.7 $\pm$ 0.3 (62)	5.2 $\pm$ 0.5 (18)	$F_{1,78} = 0.14$	>0.05
	1997	4.8 $\pm$ 0.3 (71)	5.0 $\pm$ 0.5 (19)	$F_{1,87} = 0.15$	>0.05
No. fledglings, successful nests <sup>e</sup>	1996	5.4 $\pm$ 0.2 (54)	5.6 $\pm$ 0.3 (17)	$F_{1,69} = 0.01$	>0.05
	1997	5.7 $\pm$ 0.2 (60)	5.4 $\pm$ 0.3 (18)	$F_{1,76} = 1.08$	>0.05
Mean nestling mass <sup>f</sup>	1996	9.8 $\pm$ 0.1 (36)	10.0 $\pm$ 0.2 (16)	$F_{1,127} = 1.96$	>0.05
	1997	9.8 $\pm$ 0.1 (61)	10.0 $\pm$ 0.2 (18)		
No. fledglings $\geq$ mean mass <sup>g</sup>	1997	3.6 $\pm$ 0.2 (62)	3.5 $\pm$ 0.4 (16)	$F_{1,75} = 0.03$	>0.05

<sup>a</sup> Where possible and appropriate, data for two years were combined in a single analysis that controlled for effects of year on reproduction. When a significant interaction occurred between year and pairing status, tests were made for each year separately.

<sup>b</sup> Shown are least-squares means adjusted for effect of breeding date; *F*-test from ANCOVA with first egg date as covariate.

<sup>c</sup> Successful nests produced  $\geq$  1 fledgling. *G* from log-linear test.

<sup>d</sup> Shown are least-squares means controlling for effect of clutch size from a parametric ANCOVA; *F*-test from Quade's Rank ANCOVA (Huitema 1980) with clutch size as a covariate.

<sup>e</sup> Shown are least-squares means adjusted for effect of clutch size and year from a parametric ANCOVA; *F*-test from Quade's Rank ANCOVA with clutch size as a covariate.

<sup>f</sup> Shown are least-squares means controlling for effects of year and breeding date; *F*-tests for effect of pairing status in ANCOVA with first egg date as covariate.

<sup>g</sup> Mean mass = mean mass of fledglings in 1997 (9.90 g). Data available for 1997 only. Shown are least-squares means adjusted for effect of clutch size; *F*-test for effect of pairing status from ANCOVA with clutch size as covariate.

than monogamous females to fledge at least 1 nestling (92% vs 80% of attempts, respectively;  $G_1 = 3.57$ ,  $P < 0.06$ ; Table 1). Main causes of nest failure were complete brood starvation (3% and 9% of primary and monogamous broods, respectively) and destruction of offspring following takeover of the territory

by a conspecific male (affecting 0% and 7% of primary and monogamous attempts, respectively).

There was no significant difference in the number of offspring fledged by monogamous and primary females in either year (1996:  $F_{1,78} = 0.14$ ,  $P > 0.05$ ; 1997:  $F_{1,87} = 0.15$ ,  $P > 0.05$ ; Table 1). Monogamous and primary females did not differ significantly in the proportion of eggs that they hatched successfully [ $0.91 \pm 0.03$  ( $n = 34$ ) vs  $0.92 \pm 0.01$  ( $n = 101$ );  $t_{133} = 0.59$ ,  $P > 0.05$ ], or in the proportion of hatched offspring that they fledged [ $0.91 \pm 0.03$  ( $n = 34$ ) vs  $0.89 \pm 0.02$  ( $n = 101$ );  $t_{133} = 0.59$ ,  $P > 0.05$ ]. Mean mass of offspring in primary broods was not significantly different from that of offspring in monogamous broods in either year ( $F_{1,127} = 1.96$ ,  $P > 0.05$ ).

Considering all nests, successful and unsuccessful, fledging success at primary nests was unrelated to the degree of nesting synchrony between primary and secondary nests ( $r_s = -0.02$ ,  $n = 35$ ,  $P > 0.05$ ; Fig. 4). However, the mean mass of offspring in primary broods declined significantly as the interval between the hatching of primary and secondary clutch-

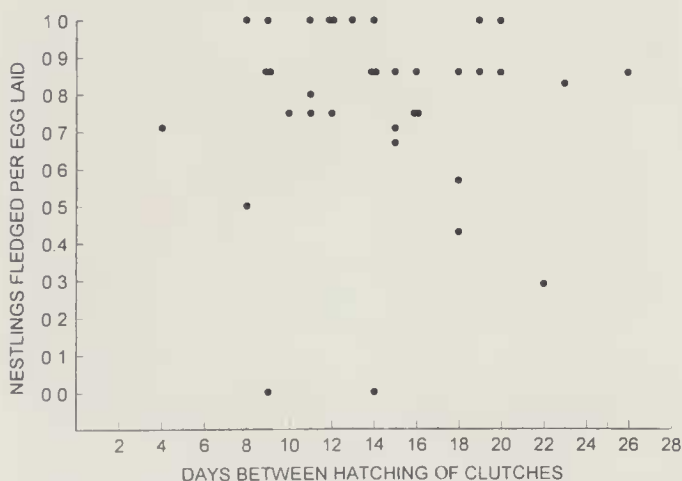


FIG. 4. Relationship between number of days elapsing between hatching of clutches of the primary and secondary female on territories of polygynous male House Wrens and fledging success (number of offspring fledged per egg laid) of the primary female (Spearman rank correlation:  $r_s = -0.02$ ,  $n = 35$ ,  $P > 0.05$ ).



FIG. 5. Relationship between number of days elapsing between hatching of clutches of the primary and secondary female on territories of polygynous male House Wrens and the mean mass of offspring produced by primary females on Nestling Stage Day 12 (Spearman rank correlation:  $r_s = -0.40$ ,  $n = 30$ ,  $P < 0.03$ ). Nestling Stage Day 1 = day clutch begins hatching.

es increased ( $r_s = -0.40$ ,  $n = 30$ ,  $P < 0.03$ ; Fig. 5).

**Reproductive output in second breeding attempts.**—A significantly greater proportion of primary than monogamous females attempted second broods in 1996 (56% vs 21% of females, respectively;  $G_1 = 5.21$ ,  $P < 0.03$ ) but not in 1997 (43% vs 63% of females, respectively;  $G_1 = 1.56$ ,  $P > 0.05$ ; Table 2). In 1996, the mean time elapsing between first and second attempts of females classified as primary

or monogamous in first attempts did not differ (35.7 vs 35.8 d, respectively;  $t_{13} = 0.02$ ,  $P > 0.05$ ). In 1997, however, primary females took significantly longer to initiate second clutches than did monogamous females (43.0 vs 37.6 d;  $t_{28} = -2.42$ ;  $P < 0.02$ ; Table 2).

There was no significant difference between primary and monogamous females in size of clutches laid for second breeding attempts in either year (1996:  $F_{1,12} = 1.94$ ;  $P > 0.05$ ; 1997:  $F_{1,28} < 0.01$ ,  $P > 0.05$ ; Table 2). Nor did we find a significant difference either year in the proportion of second attempts that were successful ( $P > 0.05$  for both years), although sample sizes for primary females were quite small in each year (Table 2). In 1996, primary and monogamous females did not differ substantially in mean number of offspring fledged from second nests ( $Z = 0.06$ ,  $P > 0.05$ ; Table 2). In 1997, however, on average, primary females fledged two (60%) fewer offspring from second nests than did monogamous females ( $Z = -1.91$ ,  $P < 0.06$ ; Table 2).

**Annual reproductive output.**—Females with monogamous and primary status in first breeding attempts did not produce significantly different numbers of fledglings over the course of the entire breeding season in 1996 or 1997 (both  $P > 0.05$ ; Table 3).

**Return rates of females.**—The probability of a female returning to our site was unrelated

TABLE 2. Comparison of reproductive output in second breeding attempts of the season for female House Wrens that had either monogamous or primary mating status in first attempts. Shown are means  $\pm$  1 SE with number of nests observed in parentheses.

Measure	Year	Monogamous females	Primary females	Test statistic	P
Frequency of second attempts <sup>a</sup>	1996	6/28 (21.4%)	9/16 (56.3%)	$G_1 = 5.21$	<0.03
	1997	25/40 (62.5%)	6/14 (42.9%)	$G_1 = 1.56$	>0.05
Interclutch interval <sup>b</sup>	1996	35.8 $\pm$ 1.7 (6)	35.7 $\pm$ 1.8 (9)	$t_{13} = 0.02$	>0.05
	1997	37.6 $\pm$ 0.9 (24)	43.0 $\pm$ 2.5 (6)	$t_{28} = -2.42$	<0.02
Clutch size <sup>c</sup>	1996	5.3 $\pm$ 0.3 (6)	4.9 $\pm$ 0.3 (9)	$F_{1,12} = 1.94$	>0.05
	1997	5.5 $\pm$ 0.2 (25)	5.5 $\pm$ 0.3 (6)	$F_{1,28} < 0.01$	>0.05
Number of nests successful <sup>d</sup>	1996	4/6 (66.7%)	9/9 (100.0%)	FET <sup>e</sup>	>0.05
	1997	19/25 (76.0%)	3/6 (50.0%)	FET <sup>e</sup>	>0.05
No. of fledglings, all nests	1996	3.2 $\pm$ 1.0 (6)	3.6 $\pm$ 0.5 (9)	$Z = 0.06$ <sup>f</sup>	>0.05
	1997	3.5 $\pm$ 0.5 (24)	1.5 $\pm$ 0.7 (6)	$Z = -1.91$ <sup>f</sup>	<0.06

<sup>a</sup> Shown is number of females attempting second broods/total number of females that presumably fledged offspring from first broods early enough to attempt a second brood (see text).  $G$  from log-linear test.

<sup>b</sup> Equals total days elapsing between the last egg of the first brood and the first egg of the second brood.

<sup>c</sup> Shown are least-squares means adjusted for breeding date.  $F$ -test for effect of status from ANCOVA with first egg date of second brood as covariate.

<sup>d</sup> "Successful" nests produced  $\geq 1$  fledgling.

<sup>e</sup> FET = two-tailed Fisher's exact test.

<sup>f</sup>  $Z$  scores from Wilcoxon Rank Sum tests.

TABLE 3. Total number of offspring fledged over the course of the entire breeding season for monogamous and primary female House Wrens. Included in analyses are all females that presumably completed first breeding attempts early enough to make a second attempt (see text for specific criteria). Not all females made second attempts. Number of nests observed are in parentheses. Shown are least-squares means  $\pm$  1 SE from ANCOVA with first egg date of first brood as covariate.

Year	Monogamous females	Primary females	Test statistic	<i>P</i>
1996	6.8 $\pm$ 0.4 (31)	6.9 $\pm$ 0.6 (17)	$F_{1,45} = 0.04$	>0.05
1997	7.5 $\pm$ 0.5 (45)	6.0 $\pm$ 0.8 (15)	$F_{1,57} = 1.70$	>0.05

to the number of broods she had reared the previous year: females returned in 40 of 137 (29%) versus 18 of 48 (38%) instances where they had reared one and two broods the previous season, respectively ( $G_1 = 1.10$ ,  $P > 0.05$ ). Including single and double brooded females in a single analysis, we saw females the next season in 43 of 146 (29%) instances where females had monogamous status the previous season versus 15 of 39 (38%) instances where females had primary status ( $G_1 = 1.11$ ,  $P > 0.05$ ).

#### DISCUSSION

We found no evidence to suggest that mate sharing reduces the reproductive output of primary females in polygynous trios of House Wrens, at least during first breeding attempts of the season when mate sharing occurs. In each of two years, primary females fledged as many offspring as did monogamous females, and offspring fledged by primary and monogamous females were of similar weights suggesting similar prospects of surviving to breed. In fact, primary females tended to be more likely than monogamous females to fledge at least one nestling because primary females lost fewer broods to starvation or destruction by conspecifics.

Primary females in our study were probably not, as a group, older and more experienced than monogamous females and hence more capable breeders. In the second year of study (1997) 50% of primary females and 48% of monogamous females had at least one year's breeding experience. Although we could not make the same comparison for 1996 (because few females were marked in 1995), we note that primary females laid significantly smaller clutches than did monogamous females in 1996 which suggests that, if anything, primary

females were less capable breeders than monogamous females this year.

Primary females may have reproduced equally as well as monogamous females during first breeding attempts of the season for reasons other than age or experience. First, mate sharing simply may not be immediately costly for primary females; i.e., all else being equal, females would usually breed equally well with or without a secondary female present. Consistent with this, rates at which males fed primary broods were, on average, not significantly lower than rates at which males fed monogamous broods.

Alternatively, there may normally be some immediate proximate costs to mate sharing for primary females but such females are compensated for these costs by having access to better-than-average territorial resources (nest sites, food, cover, etc.) or perhaps genetic resources (resulting in the production of more viable offspring; e.g., Kempnaers et al. 1992). This would allow primary females to breed as successfully as monogamous females who have, on average, lower quality breeding situations. In Chiffchaffs (*Phylloscopus collybita*), primary females appear to produce about 30% more offspring than monogamous females in part because primary females more frequently occupy higher quality habitat than do monogamous females (Rodrigues 1996). In our study, for example, access to high quality food resources might have allowed primary females to compensate for any reduction in rates at which their mates feed offspring (see also Bensch 1996).

We cannot determine whether breeding situations of primary females in our study were, on average, of higher quality than those of monogamous females. One might expect this to be the case if primary females settled ear-

lier in the season than monogamous females giving primary females a better selection of territories and mates. Primary females settled earlier than the monogamous females to whom they were compared in 1996, and bred more successfully than monogamous females in this one year. To distinguish between the "no-cost" and "compensation-for-costs" explanations for the equal success of primary and monogamous females, one would have to remove secondary females from a randomly selected group of territories and compare the success of primary females on those territories to that of unmanipulated primary females. The no-cost hypothesis predicts equal success for experimental and control females while the compensation-for-costs model predicts that experimental females would outperform control females.

Although mate sharing did not seem to affect female reproductive output during the concurrent breeding attempt, our study does suggest that mate sharing may affect female success at producing second broods in some years. In 1996, primary females were more likely to make a second breeding attempt and tended to be more successful in second attempts than monogamous females. In contrast, in 1997, primary females tended to make fewer second breeding attempts and fledged fewer offspring from those attempts when compared to monogamous females. Numbers of second breeding attempts observed each year were small, especially for primary females, and our data must therefore be viewed with some caution. Further comparisons of annual fitness in females that do and do not share mates certainly seem warranted, however.

In some polygynous species, males provide more feeding assistance to secondary females when primary and secondary nesting cycles overlap extensively and the age difference between primary and secondary broods is small. Reproductive output of primary females declines as overlap in primary and secondary nesting cycles increases in some species, for example, in Pied Flycatchers (*Ficedula hypoleuca*; Lifjeld and Slagsvold 1989, 1990) and Blue Tits (*Parus caeruleus*; Kempnaers 1995) but not others, for example, European Starlings (*Sturnus vulgaris*; Sandell et al. 1996). In our study, we found no relationship between the extent

of overlap in nesting cycles of primary and secondary females and the number of offspring fledged per egg laid for primary females. However, the mean weight of offspring produced by primary females was lowest when primary and secondary cycles overlapped relatively little. One potential explanation for this result is that if secondary females settle late, just before or just after primary eggs hatch, the fertile period of the secondary female will overlap the first part of the primary female's nestling stage when offspring require brooding and male aid is most essential (Johnson et al. 1992, Johnson and Kermott 1993). Polygynous Red-winged Blackbird (*Agelaius phoeniceus*) males are less likely to feed offspring of an early settling mate when a later settling mate is in her fertile period (as opposed to her pre- or post-fertile period; Whittingham 1994). In our study, however, feeding rates of males to primary broods seemed unaffected by the fertility status of the secondary female. Why a primary female tends to produce lighter nestlings when settlement of the secondary female comes late in her nesting cycle remains unclear.

We used nest boxes mounted on greased poles which eliminated nest predation. We chose to eliminate nest predation entirely because rates and patterns of predation on nests in boxes do not match those for nests in natural cavities, even if boxes are mounted on trees (Johnson and Kermott 1994). Under natural conditions, approximately 30% of nesting attempts on our site fail, many probably as a result of predation. Note that elimination of nest predation makes our results more conservative since more secondary females completed nesting attempts than would be expected under natural conditions; that is, we increased the extent to which some primary females had to share mates and hence increased our chances of documenting a cost of mate sharing for primary females. Elimination of nest predation might be a concern if, under natural conditions, primary females normally suffered higher rates of predation than monogamous females. However, we have no reason to suspect that nests of primary females are depredated more than nests of monogamous females.



## ACKNOWLEDGMENTS

We thank B. Beuf, K. Schuster, and the Northern Trust Co. for permission to work on the ranches comprising our study site; B. Beuf for living quarters and generous hospitality; D. Albrecht, B. Haines, K. Lago for valuable assistance in the field; and S. Bensch, J. Brawn, D. Forester, H. Kermott, J. Lifjeld, E. Scully, K. Ross, W. Searcy, W. Taylor, and K. Yasukawa for comments on earlier drafts of this paper that resulted in substantial improvements. S.C. received financial support from Sigma Xi Scientific Research Society and from the Graduate School and Dept. of Biology, Towson University.

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